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THE STUDY OF HEREDITY.

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By heredity we mean the laws governing the likeness between parent and offspring. The scientific study of heredity starts, like all other sciences, from the basis of common everyday knowledge and experience. Just as physics starts from the knowledge gained from handling of heavy objects, etc., through thousands of years, and chemistry from observations on the result of fire on stones, so our study of heredity has as its initial platform the knowledge that a child in general "takes after" its parents, sometimes resembling one parent more than another and sometimes resembling one parent in one feature and the other in another. Science, after all, consists in looking closely and consistently at the same things that the ordinary man regards carelessly and superficially.

The first thing to be investigated in heredity is the connection between parent and offspring. In the lowest and simplest organisms the parent divides in two thus yielding up its own existence in giving rise to two children. This phenomenon is known as reproduction by fission. When we ascend somewhat higher in the scale we find that the offspring is often produced as an excresence or bud on the body of the parent from which it later becomes separated. When in the animal kingdom the bud grows and begins to exhibit the characteristic features of the parent but does not separate from it, the compound system is spoken of as a colony. Perhaps one of the most familiar examples of propagation by means of buds is the strawberry plant. As all gardeners know, procumbent horizontal branches are given off from the stem of this plant.

These branches are known as runners. At the extremity of each runner there is formed a bud which proceeds to grow up into a new strawberry plant, and the runner connecting this with the parent plant dies away.

But in the human race and in the higher animals most nearly related to them, in which we naturally take most interest, we find reproduction neither by means of fission nor buds but only by the formation of what are called **germ cells**. This method is the most widely distributed mode of reproduction in both the animal and vegetable kingdoms. In all but the very lowest animals and plants it coexists with budding and fission wherever these methods of reproduction are found and it is in every way more interesting than they are. It is, therefore, of the greatest importance to the scientific student of heredity to obtain a clear conception of the nature and origin of the germ cells.

In order to clarify our ideas let us reflect for a few moments on the historical origin of the word "cell." This word was used originally to designate the chamber which housed the image of the god in a temple, but had long been transferred by popular usage to designate one of the chambers in a honeycomb in which the bee stores honey. In the seventeenth century Hooke, one of the pioneer English naturalists, whilst examining thin slices of cork by means of the primitive microscopes then available, discovered that these slices, viewed by transmitted light, showed a structure which he compared to that of a honeycomb, and to the cavities which he saw in them he gave the name of cells. A short time afterwards it was discovered. chiefly by the English naturalist Grew and the Italian naturalist Malpighi, that all living plants possessed the same structure, and the conception of a plant as a spongework of hollow cells filled with watery fluids obtained wide recognition. As investigation advanced it was pointed out that all young and active cells exhibited a layer of clear syrupy liquid lining the cell-wall, and that inside this layer was the watery fluid which constituted a drop called the vacuole, and the layer of syrupy fluid was termed the primordial utricle. Further observation showed that when this primordial utricle disappeared the cell exhibited no

further changes and could rightly be described as dead, though continuing to serve a useful purpose in the plant owing to the mechanical strength of its cell wall. Attention was thus focussed on the primordial utricle, and the name protoplasm was invented by Von Mohl in 1846 for the material of which it was composed. When various staining fluids were employed to colour this protoplasm, and thus render it more conspicuous. it was discovered that in the protoplasm of each cell there was embedded a body usually of oval shape which absorbed the stain more strongly than the rest, and held it more tenaciously. On this body the name nucleus was bestowed. It was discovered further that in young and actively growing parts of the plant the cells increased in number by a process of division, and that this division of the cell was in all cases preceded by a division of the nucleus. Meanwhile investigators had been endeavouring to discover whether the bodies of animals showed any analogous structure to that exhibited by plants; and it was soon found that these bodies were made up of a repetition of units, each of which might be described as a mass of protoplasm with a nucleus embedded in it, and to these units the name cell was extended. The cell theory, by the genius of Schwann and Schleiden (1837). was thus extended to cover the structure of all living things. The smaller and simpler animals and plants in which cell structure could not be detected were supposed to represent single cells. Although Schwann's and Schleiden's conceptions of the nature of the cell proved to be erroneous to a considerable extent they popularised the idea; but the real relationship between animal and vegetable cells was not clearly and correctly stated till 1853 when Cohn enunciated it.

It is a familiar truism that when the application of a concept is widened its content is diminished: and to this rule the word "cell" is no exception. If we take a broad survey of the matter we find that whereas the majority of vegetable cells might fairly be described as hollow cases with thick tough walls filled with watery fluid, the majority of animal cells, on the contrary, have cell-walls of excessive tenuity and consist of compact masses of protoplasm without any large central inclusions of water: further, that many of the larger cells of

animals, such as muscle fibres, may contain many nuclei. Indeed, if the study of the structure of living beings had commenced with animals the conception of the unit would not have been that of a cell, but something more analogous to a brick; and one would have compared the body to a wall composed of bricks united by mortar, rather than to a honeycomb. (Fig. 1 A and B.)

Different from one another as are the great masses of adult animal and vegetable cells, very young animal and vegetable cells resemble one another much more closely, for in the young cells of plants the cell wall is thin and the central vacuole has not as yet appeared.

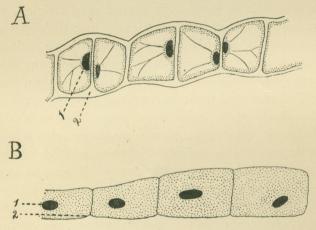


FIG. 1.

ILLUSTRATING THE DIFFERENCES BETWEEN VEGETABLE AND ANIMAL CELLS. A. Cells from the vine. B. Cells from the larva of the star-fish. 1. Nucleus. 2. Cell-wall.

As mentioned above the simplest animals and plants do not exhibit cell structure and have been supposed to be equivalent to single cells, but this is not a just way of looking at the matter. The smallest may, perhaps, be regarded as equivalent to single cells of the higher animals, but the larger, which have many nuclei, cannot be regarded in this light. They must rather be described as destitute of cellular structure. Such simple animals and plants are known collectively as **Protista**, and as they have not to any considerable extent been the subject of experiments on the laws of heredity, we may leave them out of account for the present and confine our attention to the

higher animals and plants which have well developed cellular structure.

The germ cells, as their name implies, are cells which when separated from the parent can grow into new organisms. They exhibit a considerable uniformity of structure amongst the higher animals and plants. In the vast majority of cases they are of two kinds, termed male and female respectively, and in order that a young organism should be produced it is necessary that a male cell should unite with a female cell, and so produce a compound cell which is termed a zygote. This union is termed the sexual process, and in it the nuclei of the two cells unite to form a single nucleus. In the group of plants to which the Fungi or Moulds belong, great numbers of simple germ cells are produced which can give rise to young organisms without the sexual process, as well as germ cells which must unite before development can take place. Such simple germ cells are termed conidia (Fig. 2 A), whilst to germ cells which unite the term gametes is applied, from the Greek word signifying marriage.

"Conidia" or their equivalent, are not found among the higher animals, but it occurs exceptionally amongst animals that gametes acquire the power of developing without union. This phenomenon is known as parthenogenesis. We distinguish such perverted gametes from true conidia by the fact that in shape, size and origin they resemble the normal gametes in closely allied genera, and we know that they are perverted and not original from the fact that parthenogenesis is the exception and not the rule, and appears sporadically in different cycles of animal affinity, and is by no means characteristic of primitive forms. Lastly, gametes which should undergo the sexual process may be induced to develop without it by applying artificial stimuli to them.

Returning now to the consideration of gametes which undergo the sexual process, we find that in a few cases in the lowest plants and animals they are all alike in appearance, so that male and female varieties cannot be distinguished; but, as we have already mentioned, in the overwhelming majority of cases they are divided into two categories, male and female. The male germ cell is exceedingly small and it is motile: in

almost all animals, and in the lower plants, it is provided with one or more hair-like filaments capable of rapid vibration, which propel it from place to place. In plants it is termed an antherozoid or spermatozoid (Fig. 2 B) and is provided with several of these hairs, and there is sometimes a small cell-body in which

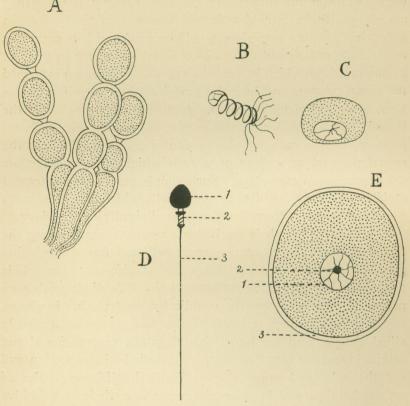


FIG. 2.

ILLUSTRATING THE DIFFERENT TYPES OF GERM-CELLS. A. The Conidia of a mould.

B. The Spermatozoid of a fern. C. The Oosphere of a fern. D. The Spermatozoon of a man. E. The Egg of a woman. The head (in D), the nucleus (in E). 2. The middle-piece (in D), the nucleolus (in E). 3. The tail (in D), the vitelline membrane (in E).

a nucleus is embedded. In animals the male germ cell is provided with a single vibratile hair which is termed the tail, and it consists besides this of a rod-like nucleus without any discoverable cell-body at all. The nucleus is termed the head, and the whole germ cell is termed the spermatozoon (Fig. 2 D). The structure of spermatozoids and spermatozoa indicates that they are

adapted to swim in fluids, and union with female gametes, or fertilization, usually does take place in a fluid medium. But in the higher plants this is not the case, and here the male cell consist of a small naked drop of protoplasm with a nucleus which becomes pressed against the female cell. Again, certain animals such as crabs, lobsters, and threadworms are constitutionally incapable of producing spermatozoa owing to the tendency of their protoplasm to produce horny matter. In these animals the male germ cells are either simple naked cells (threadworms) or cells consisting of a nucleus, having attached to it a complex horny disc which absorbs water and swells and thus pushes the nucleus into the female gamete (crabs and lobsters).

The mass of developing male gametes surrounded by a wall of protecting cells is known as an **antheridium** in plants, and as a **testis** in animals.

The female germ cell in all the higher plants and animals is a motionless cell, and it is always considerably larger than the male germ cell. In plants it is called the egg-cell, oosperm or oosphere (Fig. 2 C), in animals the egg or ovum (Fig. 2 E). The mass of developing female germ cells surrounded by a protective wall is known in plants as an archegonium, and in animals as an ovary. The female germ cell contains embedded in its substance a certain amount of unworked up food material, which serves as capital on which the zygote lives till it can feed itself. The size of the egg cell depends chiefly on the quantity of this reserve material contained in it, which in the animal kingdom is known as yolk. In birds the true egg is popularly termed the "yolk," and this in the ostrich reaches the size of a cricket ball and is the largest cell known. On the other hand the egg of a woman when it is discharged into the womb is about 126th inch in diameter, and the egg-cell or oosphere in one of the higher plants is not of any greater size. The reason for the disparity in size in these cases is the difference in the source from which the young organism derives the greater part of its nourishment. In the egg of the ostrich nearly the whole of this nourishment consists of the volk embedded in the protoplasm of the egg and hence the large size of the latter. The "white" of the egg constitutes a somewhat unimportant addition to this store. But in the case of the higher plant and of the woman the nourishment contained in the protoplasm of the egg only suffices for the first few steps in the development of the young organism. In the woman additional nourishment is supplied to the egg from the walls of the womb, and it is at the expense of this nourishment that the baby is enabled to reach its full size. In the plant the additional nourishment is supplied by a series of cells surrounding the egg-cell which are termed "endosperm," and which are absorbed as the seed develops.

Now common experience, to which we referred as the starting point of all hereditary science teaches unequivocably that the father is just as potent in transmitting his qualities as the mother. The essential hereditary element in the female germ cell cannot therefore consist of the volk or of the protoplasm in which the volk is embedded, but must consist of the nucleus, since in the spermatozoa of animals both yolk and protoplasm are absent. This comes out quite clearly when the sexual process is studied in detail. This can be easily done in the case of creatures like star-fish and sea-urchins, which produce quantities of minute transparent eggs and shed them into the sea where they are fertilized by the spermatozoa of the male. It is not difficult to watch the process of fertilization under a microscope, if a seaurchin egg be placed in a drop of sea water and some spermatozoa added. The spermatozoa propel themselves in a spiral course through the water by lashing their tails. One at last strikes the surface of the egg and proceeds to bore into it by a continuance of the same spiral motion. As soon as the "head" becomes embedded the superficial layer of the protoplasm of the egg undergoes a change and becomes converted into a skin called the vitelline membrane or primary egg-shell. This skin cuts off the "tail" of the spermatozoon and prevents any other spermatozoon from entering. Then the head pursues its way through the protoplasm of the egg swelling up as it does so, and taking on the appearance of a nucleus. It gradually approaches the nucleus of the egg and the two join to form the nucleus of the zygote. (Fig. 5 A-D.)

Since the father is just as potent as the mother we arrive at the remarkable conclusion that the nuclei of the germ cells are the transmitters of the hereditary qualities and constitute the bridge between parent and offspring.

This conclusion has not received universal assent. It has been opposed on two grounds.

- (1) That the nucleus of the spermatozoon is not the only thing to enter the egg.
- (2) That there is evidence that the beginnings of certain organs in certain embryos are situated in the protoplasm and not in the nucleus of the egg.

We shall postpone consideration of the second point and deal here with the first one.

When we look closely at a spermatozoon we can see that between head and tail there intervenes a short neck which is termed the middle piece. The middle piece follows the head into the protoplasm of the egg and there acts on this protoplasm so that it becomes the centre of a clear sphere with radiating streaks. This sphere is known as the "aster," from its resemblance to the conventional figure of a star: it comes to lie at the side of the compound nucleus of the zygote, and it plays an important part in the division of that nucleus as we shall see later. The middle piece of the spermatozoon only gives rise to a minute particle called the centrosome which lies in the centre of the aster, but it is the action of the centrosome on the maternal protoplasm which produces the aster. (Fig. 5, B, C.) Now the centrosome divides when the nucleus divides and one half goes to each daughter nucleus; it is never, so far as we know, produced from the protoplasm, but there are cases known in which it is formed anew from the nucleus. We have, therefore, every right to regard the centrosome as an appanage of the nucleus, and there is no practical difference between saying that the nucleus of the spermatozoon enters the egg and saying that the nucleus plus the centrosome of the spermatozoon enter the egg.

When once the conclusion had been reached that the nucleus is the bearer of the hereditary influence an enormous amount of attention was focussed on it. In some of the simpler

Protista, and in some cells in the higher animals, the nucleus can be seen during life; it then appears as a vesicle surrounded by a thin but clear wall and containing a clear fluid which is known as the nuclear sap. In small transparent eggs it can be easily seen and it is relatively very large: it was called by the older authors the germinal vesicle, and it contains a conspicuous solid inclusion which they called the germinal spot, but which is now known as the nucleolus.

It is only, however, when the cell is preserved and stained that the full particulars of the nucleus are seen. It is then seen to stand out from the rest of the cell by its greater power of absorbing colouring matter, and when this colouring matter is removed from the rest of the cell by dilute acid the nucleus still holds on tenaciously to it. The nuclear wall and the nuclear sap are not coloured, but the coloured portion consists of the nucleolus (when this is present) and of a series of grains of peculiar substance called chromatin, which, like beads, are strung on a series of delicate threads termed linin, which traverse the nuclear sap and are attached to the nuclear wall. In some cases the chromatin can be detected in the living nucleus as masses of denser material, and we have, therefore, no doubt that it really exists as such in the living animal, but this is not at all so certain of the linin, because the fluids used to preserve that is really to coagulate—the living protoplasm often produce cord-like precipitates in what is in life a uniform thick fluid. When a nucleus divides into two (Fig. 3), the chromatin undergoes most interesting and important changes. It seems to contract and becomes aggregated into a number of short thick rods which are known as chromosomes. It is a most wonderful thing that whenever they can be counted these chromosomes appear in the same number in all the cells of the body when the nucleus divides. This number is typically the same for all the members of the same species of animal, but varies from species to species. For reasons which will soon transpire it is termed the diploid number and is denoted by the symbol 2x. As the chromosomes become shorter and thicker the nucleolus, if there is any, is dissolved in the cell sap and totally disappears, and a little later the nuclear wall is dissolved and the nuclear sap mingles with

the protoplasm. Whilst these changes have been going on the centrosome, which lies outside the nuclear wall, has divided into two and the two daughter centrosomes have moved away from each other, each of them producing round itself an "aster" with out-streaming rays. Then each of the chromosomes is seen to be split longitudinally, and soon to each half of each chromosome a ray from one of the two asters is seen to be attached. As the daughter centrosomes continue to move apart, these rays seem to pull on the halves of each chromosome. The first effect of this pull is to cause all the chromosomes to be

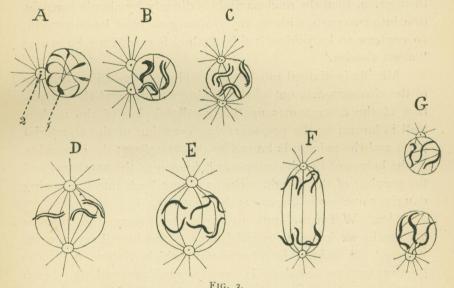


FIG. 3.

ILLUSTRATING THE PROCESS OF KARYOKINESIS (MITOSIS). A, B, C. Prophase. D. Metaphase. E, F. Anaphase. G. Telophase. 1. Chromosome. 2. Centrosome.

arranged in a plane at right angles to the line joining the two centrosomes. In this way a disc of chromosomes is formed which is known as the **equatorial plate**, and it is in this phase of division that the chromosomes are most easily counted. The fibres converging from each side of the plate to an aster constitute together a biconical figure known as the "spindle."

As the process of nuclear division proceeds the halves of each chromosome become dragged apart, each being pulled towards one of the two asters. As they separate longitudinal fibres of linin are seen to connect them. Eventually a group of

chromosome halves becomes aggregated in the neighbourhood of each aster. Then a nuclear wall is formed round each group, and so two daughter nuclei are constituted. It only remains for the chromosomes in each daughter nucleus to lengthen and gradually to lose their distinctness for the division to be completed and each nucleus to pass back into the resting condition.

This method of nuclear division is known as Mitosis or Karyokinesis. It is much the most frequent method, but occasionally when multiplication takes place in a group of specialised cells, which have no power of developing into anything unlike themselves, then the nucleus divides directly by simple constriction into two parts without any rearrangement of its chromatin. In contrast to karyokinesis this method is sometimes known as "direct division."

Mitosis is divided into phases. The gradual differentiation of the chromosomes out of the resting nucleus and the separation of the centrosomes up till the dissolution of the nuclear wall is known as the **prophase**; the formation of the equatorial plate and the spindle is known as the **metaphase**; the separation of the halves of the chromosomes is known as the **anaphase**; and the passing of the daughter chromosomes back into the resting daughter nucleus is known as the **telophase**.

Now Weismann put forward the theory that in the chromatin we have the actual bearer of the hereditary powers. "Here," he said, "is a substance which Nature takes the greatest care to distribute in exactly equal proportions to each daughter nucleus every time that nuclear division occurs, and which must be handed on from parent to offspring in unaltered proportions. Surely this must be the actual bearer of heredity."

There is a good deal of indirect evidence in favour of Weismann's view, but in provisionally adopting it we are on far less safe ground than we were when we asserted that the nucleus was the bearer of hereditary influences. The process of fertilization in animals practically shuts us up to the view that all the father's influence must pass into the zygote in the head of the spermatozoon. But to conclude that a particular element of the nucleus, which we can make distinct by our methods of staining, is the bearer of heredity is a rather dangerous assump-

tion. Nevertheless this assumption does seem to harmonise with a number of puzzling and otherwise inexplicable facts, and as more and more facts receive through it an explanation our confidence in it gradually grows.

Bearing in mind then its speculative character we shall adopt it as a working hypothesis, and shall now set forth some of the facts which support it. Of these the most important are those connected with the "ripening" or "maturation" of the germ cells. The germ cells, both male and female, when they first make their appearance are small rounded cells of somewhat denser and more deeply staining protoplasm than their neighbours. In this condition they are known as primitive germ cells, or when sex can be distinguished as spermatogonia and oogonia

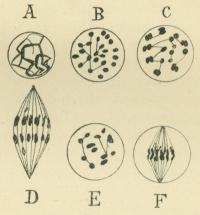


FIG. 4.

A. Prophase of the first maturation division. B. Metaphase (i.e. the equatorial plate) of the first maturation division seen from above. C. The same a little later showing the beginning of "pairing" or "meiosis." Eight "paired" and six as yet unpaired chromosomes are shown. D. The first maturation division seen from the side. E. The equatorial plate of the second maturation division seen from above. F. The second maturation division seen from the side.

respectively. They divide repeatedly and multiply rapidly in number by ordinary mitosis. After a time these divisions cease and the cells enter on a period of growth and rest, during which the distinctions between male and female cells become obvious. The male cells remain small and are known as **spermatocytes of the first order**; but certain of the female cells enlarge by devouring and absorbing many of their less fortunate sisters, and these cells are known as **unripe eggs** or **oocytes of the first order**. In both spermatocyte and oocyte the nucleus contains much sap, and in almost every case a well-marked nucleolus. (Compare Figs. 4 and 5.)

When growth is finished both spermatocyte and oocyte ripen by undergoing two divisions termed the maturation divisions. In the first of these the nucleolus disappears and the usual (diploid) number of chromosomes characteristic of the species is differentiated out of the chromatin grains. This number is in the vast majority of cases an even one. Then the chromosomes join together in pairs, so that the number is halved (Fig. 4 C). The half number is known as the reduced number, and is designated by the symbol x. In the best attested cases the junction takes place in such a way that the two chromosomes lie alongside one another and fuse into one. Subsequently a split appears in the centre of the region where the junction took place, and as the two halves of the compound chromosome still adhere at the ends it takes the form of a ring. When the equatorial plate and the spindle are formed, the two halves of the ring are dragged apart and one half ring, which corresponds to one of the original diploid chromosomes, is incorporated in each daughter nucleus. This nuclear division, therefore, differs from every other nuclear division in this, that instead of one half of each diploid chromosome passing into each daughter nucleus, some whole chromosomes go to one daughter nucleus, and some to the other. This division constitutes, therefore, an exception to the rule that there is an equal distribution of material to each daughter nucleus; it is called the reducing or meiotic division, and the process of the union and subsequent separation of two chromosomes is known as meiosis. Meiosis of perfectly typical character is found in the Protista, in the higher animals and the higher plants; it must, therefore, be of enormous antiquity, and must have originated at a time when the ancestors of existing animals, plants and Protista formed one uniform stock of lowly organisms.

In the male cell the meiotic division results in the production of two precisely equal cells which are known as the spermatocytes of the second order, but in the case of the female cell the division is unequal, and results in the formation of one large daughter cell which is known as the oocyte of the second order, and a very small daughter cell which is termed the first polar body.

The second maturation division now takes place. So far as the nuclei are concerned this is a quite ordinary case of mitosis in which each chromosome is halved longitudinally in the usual manner. In order to mark its contrast with the reducing or meiotic division it is sometimes known as the equating division, but this name is unnecessary. In the case of the male cell each spermatocyte of the second order divides into two precisely equal cells called spermatids, in the case of the female cell the oocyte of the second order divides unequally, giving rise to one large daughter which is the ripe ovum and one small daughter which is the second polar body. The first polar body usually divides at the same time into two equal daughters, but sometimes this division fails to take place. (Fig. 5.)

The polar bodies awakened much curiosity and many mysterious properties and functions were attributed to them even by Weismann, before Hertwig showed the complete parallelism of nuclear events in the male cell and the female cell. It follows that the polar bodies are nothing more than unfortunate starved sisters of the ripe egg, and the production of one big egg and three small polar bodies is another instance of that sacrifice of number to quality of which we beheld an example in the production of a few large conquering oocytes from a large number of oogonia.

When an egg has given off the second polar body it is ready to receive the spermatozoon: the nucleus which is termed the female pronucleus does not return to the resting condition until it has united with that of the spermatozoon, and, indeed, in many eggs the second maturation division does not take place until after the spermatozoon has entered the protoplasm of the egg. In the case of the male cell, however, the spermatid has to undergo considerable modification before it becomes the spermatozoon. The nucleus shrinks and expels fluid and becomes converted into an apparently solid dense mass of chromatin: the centrosome which had occupied one side of the spindle in the last maturation division gives rise to the tail filament which appears as a tiny thread growing out from it and piercing the protoplasm. Then the nucleus, dragging the tail

with it, emerges from the protoplasm which forms for a time a mantle round it; but this eventually disintegrates and is cast off, and so the perfect spermatozoon is formed.

As already mentioned, when the spermatozoon head penetrates the egg, it swells up, doubtless owing to the absorption of fluid, and forms the **male pronucleus**. Now Boveri showed that in the case of some eggs after fertilization it was perfectly possible to demonstrate in the zygote nucleus two groups of chromosomes, one derived from the female pronucleus and one

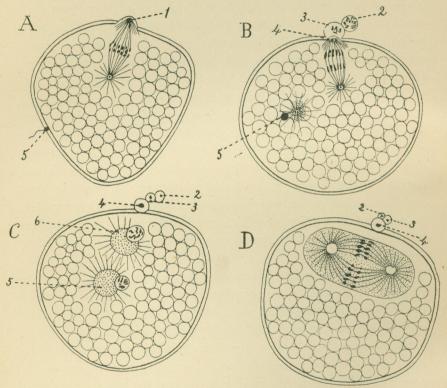
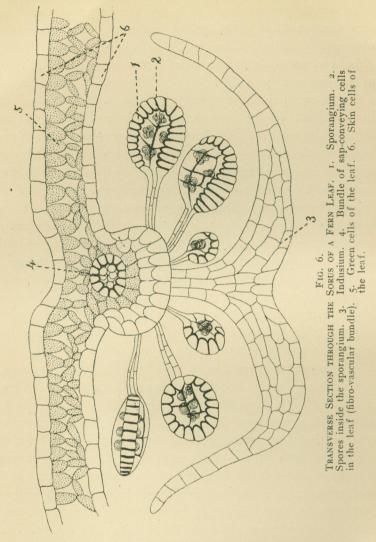


FIG. 5.

ILLUSTRATING THE RIPENING AND FERTILIZATION OF THE EGG OF A SEA-SNAIL (Crepidula). A. First maturation division which gives rise to the first polar body. The spermatozoon is just entering the egg. B. Second maturation division which gives rise to the second polar body. The first polar body has divided into two cells. The head of the spermatozoon has become the male pronucleus. C. Male and female pronuclei approaching one another each accompanied by a large aster. D. The first division of the zygote nucleus. The male and female chromosomes form two separate groups. 1. The first polar body. 2, 3. The two cells into which it divides. 4. The second polar body. 5 (in A) the head of the spermatozoon, (in B) the male pronucleus, (in C) the aster at the side of the male pronucleus.

from the male pronucleus. It is by the union of these two groups that the full or "diploid" number of chromosomes is restored. Further, he proved that when the first division of this nucleus took place, which inaugurated the development of the embryo, the plane of division cut across the line of juxtaposition of these two groups so that one half of each male and each female chromosome was distributed to each daughter nucleus (Fig. 5 D); and that the same occurred in each subsequent division so that every cell of the embryo derived half its chromosomes from the father and half from the mother. Later writers have confirmed these observations, and an American investigator, Montgomery, even went so far as to say that in each nucleus of the body the male and female chromosomes could be distinguished. Now when we recollect that the head of the spermatozoon when it pierces the egg appears to consist exclusively of chromatin and that any fluid which it afterwards acquires must be derived from the egg, we can hardly escape the conclusion that the whole of the paternal substance is represented by the chromosomes of the male pronucleus.

The course of events in the ripening of the germ cells of plants differs in many important respects from that in animals, and as the higher plants have been the subjects of most important researches on the laws of heredity, a short account of the origin of the germ cells in these plants must be given. In order to make this as clear as possible we must commence by the consideration of the case of the common fern. ordinary gardener is well aware that on the back of the graceful fronds of this plant there are to be found at certain seasons multitudes of very small dark kidney-shaped patches. Each patch is termed a sorus and is covered by a brown scale called the indusium. Underneath this scale are to be found multitudes of minute bodies of microscopic dimensions which are termed sporangia. Each sporangium is a tiny box having the shape of two watchglasses pressed together, mounted on a slender stalk. Inside the box are multitudes of excessively minute rounded bodies termed spores. (Fig. 6.) Each spore is in fact an asexual germ cell or conidium and consist of a small mass of protoplasm



with a nucleus and a thick brown cell wall. If these spores be sown on a damp brick and exposed to moderate light they will germinate after a somewhat prolonged period of rest and give rise to—not new ferns—but minute plants termed **prothallia**, which resembles little pieces of duckweed. (Fig. 7.) If we examine the structure of these prothallia we shall find that they show on the under surface numerous minute cavities, and that these cavities are of two kinds: one sort are hemispherical and the other sort

are flask-shaped. The outer walls of both kinds project very slightly above the general level of the surface of the plant. The hemispherical cavities are **antheridia** and contain the male germ cells, which in the case of the fern are spermatozoids, differing from spermatozoa in possessing several whip-like tails instead of one. The flask-shaped cavities are archegonia, each of which contains *one* female germ cell or **oosphere** surmounted by several cells situated in the neck of the flask which break up into a kind of slime. When the male cells are ripe the lid of their case breaks, they swarm forth and, swimming in the film of moisture underneath the prothallium, are attracted by the substances con-

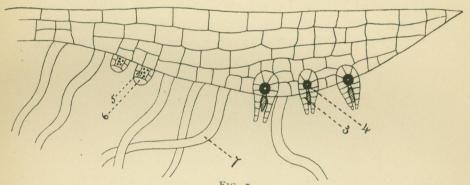


Fig. 7.

Section through the Prothallium or "Oophore" Generation of the Fern.

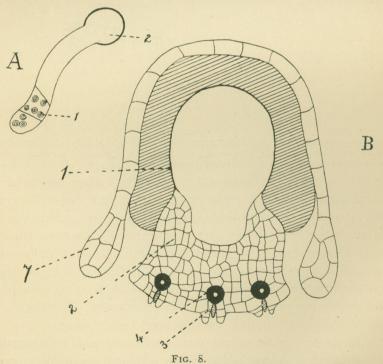
3. Archegonium. 4. Oosphere, or egg-cell in the archegonium. 5. Antheridium.

6. Spermatozoids, or male cells, in the antheridium. 7. Root-hairs of the prothallium.

tained in the slime above the egg-cells. One spermatozoid reaches and fertilizes each egg-cell. As the egg-cells ripen later than the spermatozoids, and usually many prothallia are found near each other, it will generally happen that a spermatozoid belonging to one prothallium will fertilize the egg-cell belonging to another prothallium. The fertilized egg-cell then begins to divide and develops into a young fern plant and as this grows the prothallium withers away. It follows that one prothallium can give rise to several fern plants.

In the fern plant we are thus confronted with an alternation of generations. A generation which produces spores or a spore-bearer (sporophore) is succeeded by a generation which produces egg-cells (oophore). A similar alternation of generations can be traced in all the higher plants although modified and obscured,

and we can trace a series of stages in this modification. Thus in certain water-ferns (Salviniaceæ) there are two kinds of spores produced, viz.: small spores termed microspores and large spores termed macrospores. The sporangia containing these two varieties of spores are termed microsporangia and macrosporangia respectively. The microspores on germination give rise to prothallia which bear only spermatozoids, whereas the macrospores give rise to prothallia which produce only egg-cells. These may be termed the male and female prothallia respectively. The male prothallium sometimes consists of a single filament at the end of which two cells with granular contents are cut off. These cells constitute the antheridium, and in them the spermatozoids are developed. (Fig. 8 A.) In other cases the male prothallium



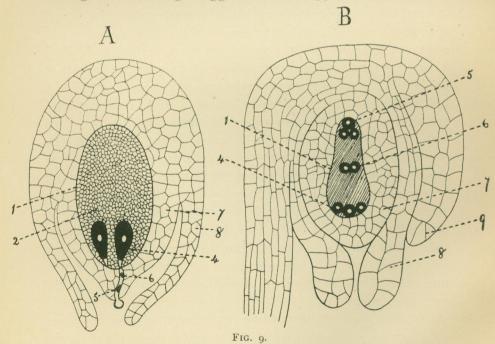
ILLUSTRATING THE GERMINATION OF THE TWO KINDS OF SPORES OF THE WATER-FERN (Salvinia). A. The germination of the microspore. 1. The spermatozoids in the vestigial antheridium. 2. The burst microspore. B. The germination of the macrospore. 1. The burst macrospore. 2. The vestigial prothallium. 3. The archegonium. 4. The egg-cell in the archegonium. 7. The wall of the burst macrosporangium.

consists of a mass of cells which hardly protrude beyond the wall of the spore. The female prothallium (Fig. 8 B), likewise consists of a mass of tissue projecting only a little way beyond the burst wall of the spore. In this mass are formed one or more archegonia in each of which an egg-cell is developed. The macrospores which produce female prothallia are larger than the microspores which produce male prothallia. Both macrospores and microspores are produced in fours by two successive divisions of a mother cell, but whereas in the formation of microspores all four sisters become spores, in the case of the macrospores only one of the four becomes a spore whilst the other three cells remain small and remind us of the polar bodies in animal eggs.

In that strange tropical plant the Cycad there is essentially the same arrangement, but the female prothallium, termed the endosperm, remains entirely within the macrospore, only one of which is produced in each macrosporangium. The macrospore is now termed the embryo-sac. In the pines and their allies we find the further modification that the filamentous male prothallium is produced only when the microspore, or, as it is now termed, the pollen-grain is wafted by the wind so as to alight on the macrosporangium, or, as it is now termed, the ovule. (Fig. 9 A.) This male prothallium consists of a filament termed the pollen-tube, at the apex of which the male germ cells are formed, but these are no longer spermatozoids, but small rounded naked masses of protoplasm, which when they escape fall directly on the slime cells in the necks of the archegonia in the female prothallium. They easily traverse the slime and fertilise the eggcells. Several young pine plants are thus formed in each embryo-sac, but only one survives, the rest perish in consequence of the withdrawal of nourishment from them by the successful one.

Finally, in ordinary flowering plants, matters are very much as they are in the pines, but the macrosporangia or ovules are enclosed in a box or case formed by conjoined leaves called the **ovary** (not to be confounded with the ovary of an animal). The tips of these leaves form the sticky surface or **stigma** on which the microspores or pollen grains fall and where they

germinate and produce the male prothallia or pollen-tubes. Each pollen tube produces only one male cell. The female prothallium is represented only by eight cells, devoid of cellwalls, embedded in the protoplasm of the macrospore or embryo-sac-these are produced by three successive divisions of the macrospore nucleus. Of these, three are situated in the upper part of the macrospore where the contact with the pollentube takes place, three termed antipodal cells at the lower end, and two in the middle. These last two coalesce to form a single cell termed the mother cell of the endosperm. The endosperm is a nutritive tissue formed by the division of this mother cell after fertilization which fills up the cavity of the macrospore, and very possibly does not correspond to the endosperm of cycads and pines. Of the six remaining cells only one is a ripe egg-cell, and is fertilized by the male cell, the remainder are to be regarded as vestigial egg-cells and disappear. (Fig. 9 B.)



Longitudinal Section through the "Ovules" or Macrosporangia of the Seed-Plants. A. Section through the ovule of a Pine. 1. Macrospore or embryo-sac. 2. Endosperm or prothallium inside embryo-sac. 4. Archegonium. 5. Pollen-tube in male prothallium. 6. Male nucleus in pollen-tube. 7. Macrosporangial wall. 8. Envelope surrounding macrosporangial wall. B. Section through the ovule of a flowering plant. 1. Embryo-sac. 4. Egg-cell and its two sister cells. 5. Antipodal cells. 6. Endosperm-forming cells. 7. Macrosporangial wall. 8. Inner, 9, outer, envelope of macrosporangium.

It follows that only one embryo plant is formed in each macrospore or embryo-sac, and this baby plant, surrounded by the endosperm and the remains of the macrosporangium or ovule, forms the seed. It is the merit of Professor Farmer to have shown clearly that in all these higher plants the all important meiotic or reducing division does not occur during the formation of the sexual germ cells, but during the formation of the spores. The nuclei of all the cells of the prothallia produced by the germination of the spores have therefore the reduced number of chromosomes, and this is equally true of the comparatively large prothallia of ferns, and of the vestigial prothallia of the pines and flowering plants. The germ cells produced by these prothallia have likewise the reduced number, and, as in animals, the diploid number is restored by the act of fertilization.

It is well, however, to emphasize the fact that what we call a seed really comprises parts of two generations; within is the embryo plant consisting of rootlet and seed-leaves or cotyledons which constitutes one generation, whilst without is the testa or seed-coat. This is the macrosporangial wall, which being part of the maternal tissues belongs to another generation. The endosperm is often entirely absorbed by the embryo before the seed is ripe as in the common pea, but sometimes it persists as in Indian corn; it, too, is part of the maternal generation, but since its mother cell is formed by the fusion of two other cells its nuclei have the full number of chromosomes.

We should be doing our readers an injustice if we allowed them to think that the account which we have given of the meiotic or reducing division was universally accepted. Some investigators maintain that there is no pairing of chromosomes, but that before the first maturation division half the usual number of chromosomes are formed from the chromatin grains in the resting state. There are a few cases, however, where the pairing can be seen with startling clearness, and these cases make it almost certain that pairing occurs in other cases also. Then, again, many investigators maintain that chromosomes pair end to end, and not side by side, but it appears that end to end pairing when it occurs is merely the

first stage in side by side pairing, that in fact the two chromosomes touch at one point and then swing round so as to be parallel to one another.

It must be borne in mind that only in cases where the chromosomes are few and large can the sequence of events be satisfactorily made out. When, as usually happens, they are very numerous and small, differences of interpretation are very frequent. The view which we have given in the preceding pages is the one endorsed by those who have studied these clear cases.

When the germ cells have united with one another and the zygote has been formed, it has, of course, a long period of development to undergo before it attains the adult form. From this development some important facts can be gleaned about the nature and mechanism of heredity. This is especially true of animal development, and we may now indicate a few general points in the nature of this.

The egg of one of the higher animals begins its development by dividing into a number of cells—this process is known as segmentation. Then these cells are moulded by folding, into the primary organs or germinal layers. Of these there are three, viz., the ectoderm or primary skin, the endoderm or primary gut-wall, and the mesoderm or primary lining of the bodycavity. This process is known as the formation of the layers. Finally, these primary organs by processes of growth and folding give rise to the secondary organs, thus, for example, the ectoderm gives rise to the outer layer of the skin, the nervous system and the sense organs, the endoderm to the liver, pancreas and lungs as well as to the lining of the alimentary canal, whilst the mesoderm forms the bones and muscles. This process is known as organogeny.

The growing organism during the first part of its existence is sheltered from outside influences either by an eggshell, or by being retained within the mother's body, or in rare cases by being taken into cavities in the father's body. During this period it is called an embryo. When it finally escapes into the outer world it is still in many cases very unlike the parent, and has to undergo a series of changes or metamorphoses before it attains the adult form; during this period it is known as a

larva. The best known example of a larva is the tadpole of the frog. Now every animal begins its existence by being an embryo, and it may be fairly said that every animal later becomes a larva, for none leaves the eggshell or the body of the parent with the proportions and powers of the adult. The small boy can be justly characterised as a human larva, for in body, but still more in mind, he is different from the adult. The relative importance, however, of the embryonic and larval stages varies greatly. Sometimes the development is mainly of the embryonic type and sometimes of the larval type.

Now the startling thing about some larvæ is that they are unquestionably reproductions of a former state of the race to which the parents belong. This will become clear when some examples are given. Thus, as everyone knows, the vast majority of fish are bilaterally symmetrical animals, that is to say that in them the right and left sides resemble one another as an object resembles its image in the mirror. But in a small but very important group of fish (the flat-fish) this is not so. These fish swim lying on one side. On the side directed upwards are both eyes, and the mouth is often unevenly placed, the greater part being directed downwards. The larvæ of these fish are, however, symmetrical, for in them each side has its eye and the mouth is straight in front. Again, the overwhelming majority of bivalve molluscs burrow in the mud, and possess for this purpose a muscular tongue-like appendage termed the foot, which they protrude from between the valves of the shell. The oyster, however, is an exception to the rule, for it lies throughout life on one side and possesses no foot. But the American oyster when young creeps about and possesses a tongue-like foot. Still one more example of this phenomenon may be given. The majority of those exquisite marine animals, the feather-stars or "lily-encrinites," are extinct, but we learn from their fossilised remains that nearly all of them during life were rooted to the bottom by long stalks. Some of the living species show the same structure. The commonest form, however, has no stalk when adult and possesses the power of swimming from place to place, but when it is young it is rooted to the bottom by a stalk exactly like its fossil relatives. When

it approaches maturity it breaks loose from its stalk and swims free. In the case of these larvæ we may say that the life history "recapitulates" the history of the race.

The discovery of cases like these fired the imagination of zoologists thirty years ago, and for some considerable time one main preoccupation of zoological research was the attempt to reconstruct ancestral history from a study of the life history. Unfortunately, the recapitulatory element, as we may call it, is not the only influence which moulds the life history, other influences which modify and obscure the ancestral element are at work, and the disentanglement of the parts played by the various influences is no easy matter. The attempt to do so led to much wild speculation and mutually contradictory hypotheses, and the apparent impossibility of arriving at certainty in the matter resulted in the disparagement of the whole idea.

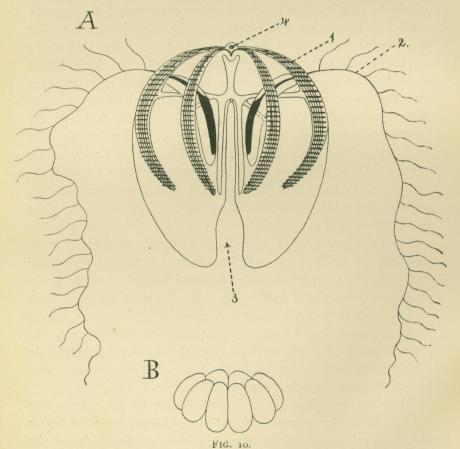
But if there be any truth in the idea that there is a recapitulatory element in development, we simply cannot afford to ignore it if we are attempting to elucidate the laws of heredity. For the recognition of this element implies this: that when an animal changed its mode of life and sought a new environment and new ways of acquiring food, this usually happened at adolescence, and the new structures which were at first acquired as a reaction to the environment became, in course of time, so fixed in the animal's constitution that they appeared at progressively earlier periods in the life history and eventually independently of the environment at all.

Of course, our critic might maintain that we have no proof that the ancestors of the flat-fish ever were like ordinary fish, or that the ancestors of the oyster ever burrowed, or, finally, that those of the feather-star were ever permanently fixed. The only conclusive proof would be furnished if some angelic recorder had watched the transformation slowly proceeding, and had left a duly attested account of the whole thing. As Huxley has said: "If a man chooses to assert that a fossil shell is a mineral concretion it is impossible to drive him from his position by logic." But the fact that in the three cases mentioned no naturalist, however much he might inveigh against recapitulatory interpretations in general, would question the

ancestral significance of the larva is proof enough for most sensible people. Exactly the same kind of proof convinces people that Frauenhofer's lines in the solar spectrum, and similar lines seen in the spectra of heated metals, are due to the same cause.

Once it is understood that the larval phase is often a partial reproduction of some bygone condition of the race, the relation of the embryonic phase to it becomes plain. The embryonic phase is a modification of the larval phase. Taking the tadpole as a typical larva, we find that all its organs are adapted for life in water. Now there is in the island of Martinique a toad which is hatched from the egg as a toad. If we examine what goes on within the egg, we find a tadpole whose organs under embryonic conditions are useless and only comprehensible if we allow that in a former condition of the race the tadpole escaped from the egg and lived in the water. It is often asked if the development of animals be a partial recapitulation of the history of the race why the ancestral history of plants should not be revealed by their life history. The answer to this is twofold, first, sharply marked larval phases are found where an animal changes its environment and lives during the earlier part of its life under one set of conditions, and the later under another set, and the earlier set of conditions then represents what was the environment of the adult in the ancestral state of the race. A plant cannot move from one environment to another during its growth, so when the surrounding conditions change they generally leave their impress on the plant from its first appearance above ground and leave little or no room for a larval stage. Secondly, in some few cases plants have a larval stage, or, as botanists term it, a "youth-form." The common gorse, in which green thorns replace leaves, has, when young, leaves like other plants, but these drop off as it grows older, and the Australian Acacia, in which flat green leaf-stems take the place of leaves, has likewise leaves like those of other acacias when young.

But the question of the recapitulation of the ancestry of the race is not the only one which is raised by the contemplation of the development of the egg. When we watch under the microscope the organs being formed in the delicate transparent germ giving, to quote the simile used by Huxley, the appearance of the work of an invisible finger moulding the embryo into the lineaments of the animal, we cannot forbear to ask ourselves how the marvel is accomplished. When an egg divides into two cells is all the material for the right side separated from that for the left? If the nuclei in the embryo could be disarranged would an abnormal creature result? The endeavour to answer questions like these constitutes the science of experimental embryology. The principal objects which have been experimented with are the eggs of frogs, sea-squirts molluscs, thread-worms, starfish, sea-urchins, and comb-bearers (Ctenophora). Driesch has shown that when a sea-urchin's egg



ILLUSTRATING THE STRUCTURE AND DEVELOPMENT OF A COMB-BEARER (Ctenophore).

A. Adult form. r. "Rib." 2. Tentacle. 3. Mouth. 4. Apical sense organ.

B. The eight-cell stage in the development of the embryo.

divides into two cells, if these cells be separated by violent shaking, each will develop into a perfect animal of reduced size. The same result is obtained if one of the first four cells be separated from the rest, and even occasionally if one of the first eight cells be separated from the rest. But on the other hand if we take the eggs of the comb-bearers (Fig 10) we get a different result. These animals are shaped like elongated grapes. They pass their lives swimming in the sea, they are perfectly transparent, and they move by the aid of eight meridians of delicate comb-like structures which converge to meet at the upper pole where there is situated a delicate brain and sense organ. Each "comb" consists of a short transverse row of cilia or vibratile hairs united at the base but free at the tips. Each row of combs is known as a rib. As the Ctenophora come to the surface in a calm sunlit sea, these combs glisten with the most lovely iridescent colours, and the whole creature presents a spectacle of great beauty. The first stage in the development of these animals is that the egg divides into eight cells ranged in a circle. (Fig. 10 B.) From each cell one-eighth of the animal including one rib, is developed. If we remove one of these eight cells the remaining seven give rise to a creature with seven ribs, if we remove two a creature with six ribs is produced, and so on.

How are these differences in the constitution of the two eggs to be accounted for? The most plausible explanation which has been put forward is that there exist **organ-forming substances**, and that in each cell of the ctenophore there is a substance which contains the materials necessary for the formation of a particular rib. In each of the first eight cells of the segmenting sea-urchin egg, on the contrary, there is the same kind of substance, so that any one of them contains the necessary materials for constructing the whole body.

The question then arises, in what part of the cell are these materials to be found, in the protoplasm or the nucleus? Now Driesch has shown that if a fertilized egg of a sea-urchin be allowed to develop under such pressure as is produced by being squeezed between two glass slides, the first eight cells instead of forming two tiers of four each as they do in the normal egg,

are all spread out in one plane. If now the pressure be removed the eight cells divide into two tiers when the sixteen cell stage is reached, and this mass of cells is capable of developing into a perfectly normal animal, although the nuclei which should have formed the lower pole are now situated at the sides. nuclei can therefore be juggled about like a handful of marbles without altering the course of development, and therefore the peculiar organ-forming substances must be in the protoplasm and not in them. This result is confirmed by some experiments which Driesch made on the ctenophore egg. He cut pieces from these eggs before they had divided into cells at all, and he showed that when these mutilated eggs survived they gave rise to imperfect animals, in which the full number of ribs was not produced. The specific organ-forming materials for the ribs must be in the protoplasm, for there was as yet only one nucleus and it was not touched by the operation.

These quite unexpected results were seized on by those who opposed the view that the nucleus was the sole bearer of the hereditary qualities as confirmatory of their objections. Of course, even if we admit that the bases for the qualities which the young animal inherits from its mother are situated in the protoplasm and not in the nucleus, we have still to face the difficulty that the evidence compels us to believe that all qualities inherited from the father are carried in the head of the spermatozoon which is a nucleus.

Fortunately, further experiments enable us to get over this apparent contradiction in the constitution of the two kinds of germ cells. The egg of the thread-worm is a very specialised object. At its first division it gives rise to two cells, one of which is clear and the other granular. The clear cell gives rise to a part of the skin and to the nervous system, the granular cell to the internal organs. If the fertilized egg, however, be fixed to the rim of a horizontal wheel so that its axis of symmetry points towards the centre, and be allowed to develop whilst the wheel is kept in rapid rotation, it will divide into two granular cells and will develop into a double monster with two sets of internal organs, which cannot survive. It is obvious that the centrifugal force has caused the equal distribution of the

organ-forming materials between the two cells, so that each in developing must give rise to the same result.

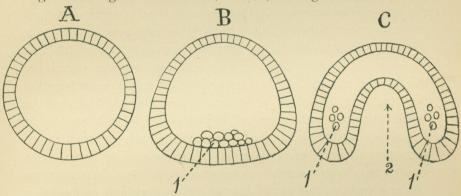
But if the same treatment be applied to the unfertilized egg we find that it can lose large portions of its protoplasm and become much reduced in size, but that nevertheless if it be afterwards fertilized it will develop into a normal embryo. Its protoplasm is, therefore, homogeneous, and we can only attribute its subsequent heterogeneity to materials given off from the nucleus which give rise to the different organ-forming substances.

This hypothesis is completely borne out when we examine the egg of the sea-squirt. Here also we find strongly-localised organ-forming substances. Indeed, in one species they are distinguishable in the living egg by their different colours. If we examine the ripening egg we find that streams of minute granules of chromatin are pouring into the protoplasm from the nucleus. We, therefore, arrive at two conclusions, first, that the nucleus of the female germ cell is just as much the bearer of the hereditary qualities as is the nucleus of the male germ cell; and, secondly, that the protoplasm of the growing egg becomes, in many cases, organised into substances which are the rudiments of the organs of the future animal by the emission of materials into it from the nucleus.

Once the protoplasm has been organised in this way, the nucleus ceases for a time to have any further influence, but after the first formed organ-forming substances are used up the nuclei at a later period of development resume their active rôle.

A beautiful instance of this occurs in the development of the sea-urchin. When the egg has divided into about 1,000 cells these form a little hollow balloon or vesicle known as the blastula. (Fig. 11.) Then one side of the blastula becomes flattened and cells termed mesenchyme cells are budded from the flattened area and pass into the interior. Immediately afterwards the rudiment of the future gut is produced by the pushing in of one side of the blastula as if by an invisible finger. The inturned portion forms the lining of the gut, and the embryo is now termed a gastrula. Now Driesch has shown that the blastula may be cut into pieces with a fine pair of scissors, and each

piece if above a certain minimal size will develop into a perfect animal. But if the operation be repeated after the mesenchyme has been produced this is no longer the case: then fragments of the blastula will, indeed, heal up and produce smaller blastulæ, but these are incapable of further development—only the piece taken from the region where the mesenchyme has been produced can form a gut. The wall of the blastula, which was at first homogeneous, has now become heterogeneous, and this differentiation is accompanied by a renewed emission of chromatin grains from the nuclei into the protoplasm. These organ-forming substances are, indeed, amongst the most strik-



THREE STAGES IN THE DEVELOPMENT OF THE EGG OF A SEA-URCHIN. A. The blastula stage. B. The formation of mesenchyme cells. C. The gastrula. 1.

The mesenchyme cells. 2. The gut.

ing discoveries of biological science, and we are as yet only on the threshold of our knowledge of them. Whether a certain mass of such a substance will give rise to one organ or two of the same kind seems to depend on its shape. If, for instance, we take the egg of a frog and allow it to divide into two cells, and then clamp it between two slides and reverse it, we may get a double-headed or a double-tailed tadpole. If we do the same with the egg of the newt we may get a complete double embryo. What is the explanation of this phenomenon? We have added nothing and removed nothing, we have in fact only turned the embryo upside down. The answer to this conundrum is that in the frog's egg there are two organ-forming substances which stand in a fixed spatial relation to one another, because of their different specific gravities, so that if the egg be turned upside

down they sort themselves out under the influence of gravity. But if the egg be turned upside down when it has divided into two cells, then since the contents of these cells are to a certain extent cut off from one another, the materials in each tend to sort themselves in the same way as if each cell were a separate egg, and hence the tendency to produce two embryos.

Another instance of the same thing can be seen in the tail of the lizard. When this is broken off a little bud is formed on the surface of the stump by which a new tail is produced. If the surface of this bud be slightly indented by the prick of a knife it will produce two tails.

When once the primary organs have been formed, they seem to emit substances which act on each other and produce further modifications by which the secondary organs are formed.

One instance of this must suffice. All students of animal biology are aware that the type of eye found in man and the higher vertebrates is a complex organ consisting of two main portions, one formed as an outgrowth from the brain and constituting the retina, and one formed as an ingrowth from the skin and constituting the lens. The retinal portion appears first in development, and in the embryo of a newt if this portion be cut off and planted under the skin in another part of the body it will cause the skin above it to form a lens. We are, therefore, driven to the conclusion that the formation of a lens in the normal development of the newt is not due to a special quality of the skin in the region of the head, but is the result of the modification of the skin in this place under the influence of the growing retina beneath it.

To sum up, the bearers of hereditary influence are the chromosomes of the nuclei of the male and female germ cells. These chromosomes are brought together in fertilization, and cause the development of the offspring by the emission of substances into the protoplasm which change its character and confer on it the power to develop into the primary organs. These primary organs in turn emit materials into the fluids of the body which affect parts of other primary organs so as to give them the power of developing into the secondary organs, and so the adult form is attained.

END OF PART I.